NOTE / NOTE

Water content and reserve allocation patterns within the bulb of the perennial geophyte red squill (Liliaceae) in relation to the Mediterranean climate

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Abstract: The patterns of water content and reserve allocation in the bulb parts of red squill (*Urginea maritima* (L.) Baker) and the plant's adaptive strategy to Mediterranean climate (Crete, Greece) were investigated. The different bulb parts serve varying ecological functions in terms of their resources and their importance for these functions. The basal plate is the active centre, developing one or two apical meristems and roots in autumn, as well as the flowering bud in late summer. The middle of the bulb (approximately the third bulb scale) stores the resources and the tunics (the outer covering structures) that provide mechanical defense. The water content and reserve allocation patterns synchronize the plant's phenological development with the seasonality of the Mediterranean climate. The adaptive strategies are based on the development of a deciduous semisubterranean life form primarily for the avoidance of drought, herbivores, and other environmental hazards, as well as nutrient shortage. The presence of cells containing lipids, polysaccharides, raphides, water, mucilage, bufadienolides, the presence of sclerenchyma, the tightly packed epidermis, and the presence of the tunics facilitate this.

Key words: bulb, geophytes, Mediterranean climate, *Urginea maritima*, water content.

Résumé : Les auteurs ont examiné les patrons de teneur en eau et l'allocation des réserves dans les parties du bulbe du *Urginea maritima* (L.) Baker, ainsi que les stratégies d'adaptation de la plante au climat méditerranéen (Crête, Grèce). Les différentes parties du bulbe servent différentes fonctions écologiques, en termes de ressource et de leur importance pour ces fonctions. La plaque basale constitue le centre d'activité, développant à l'automne un ou deux méristèmes et des racines, ainsi que le bourgeon floral à la fin de l'été. Le milieu du bulbe (environ la troisième écaille du bulbe) emmagasine les ressources, et les tuniques (structures enveloppantes externes) servent à la défense. La teneur en eau et les patrons d'allocation des réserves synchronisent le développement phénologique de la plante selon le caractère saisonnier du climat méditerranéen. Les stratégies d'adaptation reposent sur le développement d'une forme vitale décidue semi-souterraine, surtout pour éviter la sécheresse, les herbivores et les autres aléas environnementaux, ainsi que l'emmagasinage des nutriments. Ceci est facilité par la présence de cellules contenant des lipides, polysaccharides, raphides, eau, mucilage, bufadienolides, la présence de sclérenchymes, l'épiderme bien serré et la présence de tuniques.

Mots-clés : bulbe, géophytes, climat méditerranéen, *Urginea maritima*, teneur en eau.

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Introduction

Evolution of geophytes in climatic areas with marked seasonal changes has led to their adaptation to periods of high and low temperatures and (or) drought. To survive extreme environments, geophytes have undergone adaptations that may include increased capacity for water binding, tolerance of and (or) resistance to desiccation and drought, and development of subterranean organs that contain specialized storage compounds (De Hertogh and Le Nard 1993; Kamenetsky et al. 2003, 2005). A variety of carbohydrates, including starch, soluble sugars, glucomannans, and fructan are variously present in the underground storage organs of geophytes (De Hertogh and Le Nard 1993; Miller et al.

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1997). In addition, there is a possibility that some storage proteins act as a temporary store for nitrogen in several perennial species (Bewley 2002; S. Al-Tardeh, unpublished data) and are reutilized to support plant growth (Cyr and Bewley 1989, 1990)

Urginea maritima (L.) Baker has value as an ornamental, flowering after almost 6 years from germination (McCorohan 1990), when the bulb reaches a critical mass (Pascual-Villalobos and Fernandez 1999). It is also a deciduous plant possessing leaves with mesophytic characters that optimize its adaptation to the seasonal fluctuation of the environmental conditions of the Mediterranean climate. This optimization occurs by protecting the plant from environmental hazards and herbivores and by abundant production of nutrients over a short period (rainy season; Al-Tardeh et al. 2007). The roots of *U. maritima* play an important role in storing and utilizing water and nutrients (Al-Tardeh et al. 2006). The bulb, which is usually only half buried in the soil, is tunicated and mostly globular. It can reach 5–15 cm in diameter and consists of fleshy, smooth scales (modified leaf bases) that overlap one another. It has little odour, but its inner scales have a mucilaginous, bitter, acrid taste, owing to the presence of bitter glycosides. Extracts of the bulb scales of *U. maritima* contain a variety of reserves such as cardiac glycosides of the bufadienolide type (Kopp et al. 1996), which are the major glycoside constituents, anthocyanins (Vega et al. 1972), flavonoids (Fernandez et al. 1972), fatty acids, polysaccharides (Spies et al. 1992), and calcium oxalate (Cogne et al. 2001).

The order in which the different organs of plants are differentiated is important. When the leaves are differentiated before the floral parts, growth is usually synanthouş i.e., the foliage is produced before flowering such as in *Hyacinthus*, *Lilium*, *Narcissus*, and *Tulipa*. However, in some genera or species the flower bud is initiated before the vegetative bud that produces the leaves. This generally leads to the production of hysteranthous plants, i.e., flowering takes place in the absence of foliage and before leaves emerge. The synanthous pattern of flowering occurs in late spring, whereas the hysteranthous pattern occurs at the end of summer (De Hertogh and Le Nard 1993).

In hysteranthous plants, the photosynthesis rate is very low from flower emergence until anthesis. The bulb reserves are sufficient to allow flower stem elongation and flowering. The contrast to hysteranthous growth is proteranthous growth, i.e., the foliage dies down before the flower is produced (e.g., *Boophane haemanthoides* Leighton (Du Plessis and Duncan 1989). Thus, all photosynthesis takes place before flowering.

Depending on the basis of their storage organs and life cycles, two patterns can be distinguished among hysteranthous geophytes: the "*Urginea* type" and the "*Crocus* type". In the hysteranthous geophytes of *Crocus* type, such as *Crocus*, *Merendera*, *Colchicum*, and *Sternberhia*, the capsula is kept below the ground level during the winter and is protected from winter damage. The capsula is a dehiscent, dry fruit that is made up of several parts or carpels and opens to discharge the seeds. Seed dispersal starts in spring, and they go into dormancy for up to 1 year. The first chance for germination is during the following autumn. The hysteranthous geophytes of *Urginea* type, such as *Scilla autumnalis* L., *Scilla hanburyi* Baker, *U. maritima*, *Urginea undulata* (Desf.) Steinh., *Pancratium maritimum* L., and *Pamianthe parviflora* Meerow, are of tropical origin and are characterized by possessing perennial storage organs, a distinct flowering stem, seed dispersal immediately after flowering, and germination without dormancy. Indeed, this prevents the risks of long seed exposure to environmental hazards and allows for the exploitation of pollinators during autumn (Dafni et al. 1981; De Hertogh and Le Nard 1993; Al-Tardeh et al. 2007).

Previously, we conducted detailed studies on the anatomical features of the roots (Al-Tardeh et al. 2006) and the leaves (Al-Tardeh et al. 2007) of *U. maritima* as adaptive strategies for this species to the Mediterranean climate. In this study, we examine the water content and allocation patterns of reserves in the bulb parts of *U. maritima* to gain a better understanding of aspects of this species' life history such as maintenance, growth, and reproduction. The ultimate goals are to identify the structure and the function of the bulb and to suggest reasons for the abundance of the plant in the Mediterranean region. More specifically, the objective of this study is to explore the plant's efficiency in water and reserve storage during the long summer drought and its defense mechanisms against herbivores and other environmental hazards.

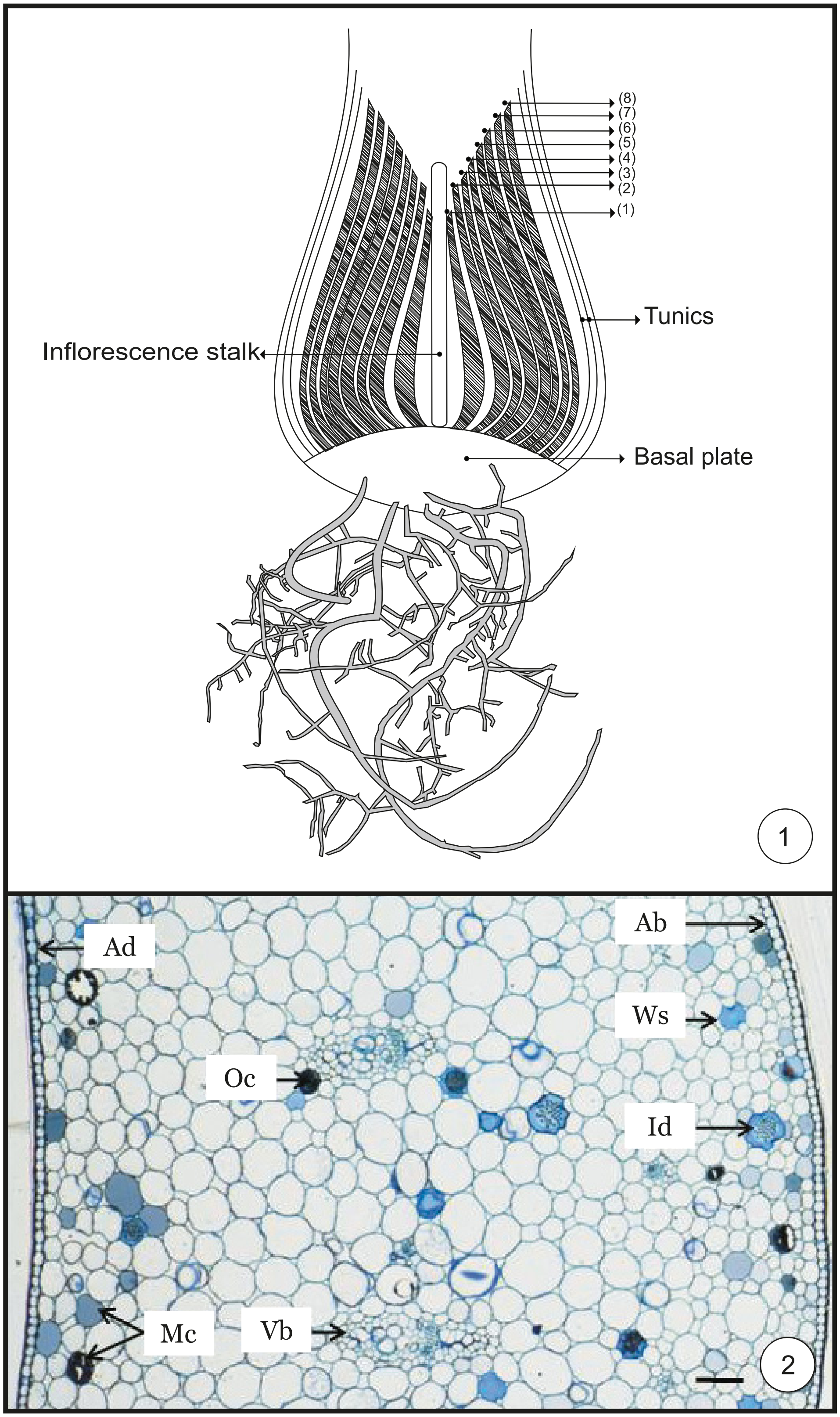
Materials and methods

Study site and plant material

The study site was located at Souda (35°33′N and 24°07′E), a town about 10 km south of Chania, on the island of Crete (the fifth largest Mediterranean island), southern Greece. Souda's climate is of the Mediterranean type and most of its annual rainfall occurs in autumn–winter, while the summer is very hot and dry. The mean annual air temperature is 18.1 °C. January (mean temperature, 10.8 °C) and February (mean temperature, 10.8 °C) are the coldest months, whereas July (mean temperature, 26.3 °C) and August (mean temperature, 26 °C) are the warmest. It is also characterized by high humidity and low barometric pressure owing to the close location to the sea and the mountains.

Individuals of *U. maritima* with a bulb diameter of 10 cm, growing wild in Souda, were collected at the end of the spring of 2005, soon after the seasonal dieback of the leaves. This particular period was chosen for three reasons: (*i*) to quantify the total nutrient content in the bulb's component parts available for reproduction and growth; (*ii*) by this time the plant has recycled the resources from the herbaceous aboveground plant parts for reusage; and (*iii*) it is before inflorescence initiation begins in early September. The bulbs were sectioned through their longitudinal median axes to determine their chronological age for the selection plants of the same age. The bulb scales were ordered from one to eight followed by the tunics, which are bulb scales that are completely dry. They were dissected from the basal plate, grouped according to their positions, and dried at 70 °C until a constant mass was obtained. The water content of constituent bulb parts was measured: (fresh constituent bulb part mass – dry constituent bulb part mass / fresh constituent bulb part mass) × 100, according to Cappelletti (1954).

Figs. 1–2. Fig. 1. Diagram of a longitudinal section of an *Urginea maritima* (L.) Baker bulb sampled from a natural population in Souda, Crete (Greece). The bulb scales are ordered from one to eight followed by the tunics and the basal plate. Fig. 2. Light microscopy (LM) micrograph of a transverse section of the middle of a bulb (third bulb scale) of *U. maritima* showing the abaxial (Ab) and adaxial (Ad) epidermises and cells with storage characteristics. (Oc, oil cell; Ws, cell with water-storage character; Id, idioblast cells containing raphides; Mc, mucilage cell; and Vb, vascular bundle). Scale bar = 10 µm.



Figs. 3–8. Fig. 3. LM micrograph of a transverse section of the basal plate of an *U. maritima* bulb showing idioblast cells containing raphide bundles. These cells are oriented in different directions. Scale bar = 10 µm. Fig. 4. LM micrograph of a fresh hand-cut transverse section of an *U. maritima* bulb scale showing cells containing soluble polysaccharides stained red with Schiff's reagent (arrows). Scale bar = 100 µm. Fig. 5. Idioblast cells (arrows) of an *U. maritima* bulb scale containing a bundle of raphides embedded in polysaccharide that has stained red with Schiff's reagent. Scale bar = 10 µm. Fig. 6. Numerous cells (arrows) of an *U. maritima* bulb scale containing lipids stained brown to black with Sudan black B. (Mc, mucilage cell; and Oc, oil cell). Scale bar = 10 µm. Fig. 7. Cells within a vascular bundle of an *U. maritima* bulb scale have reacted positively with Sudan black B. (Sc, sclerenchyma fibers; Oc, oil cell; X, xylem; and Ph, phloem) Scale bar = 10 µm. Fig. 8. LM micrograph of a transverse section of the basal plate of an *U. maritima* bulb with idioblast cells (arrows) containing bundles of raphides embedded in polysaccharide that stained red with Schiff's reagent. Scale bar = 10 µm.

Light microscopy (LM)

Segments of bulb parts were fixed for 3 h at room temperature in a mixture of 2.5% glutaraldehyde and 2% paraformaldehyde fixative (Karnovsky 1965) in 0.1 mol/L sodium cacodylate buffer, pH 7.1. After postfixation in 1% osmium tetroxide for 3 h at room temperature and dehydration in an ethanol series, the samples were embedded in Agar low viscosity resin (LV). Semithin sections (1 µm thick) were cut on a Reichert Om U_2 ultramicrotome. After staining with 0.5% toluidine blue O in 5% borax solution (Pickett-Heaps and Northcote 1966), they were photographed using an inverted photomicroscope (ECLIPSE TE2000-S, Nikon).

Bulb histochemistry

To stain lipophilic substances, semithin sections of fixed material or hand-cut sections of fresh bulb scales were stained with 1% Sudan black B and 2% osmium tetroxide (Bronner 1975; Sawidis et al. 2005; Al-Tardeh et al. 2006; 2007), respectively. For the identification of phenolic compounds, which, as artifact, also have a positive reaction to Sudan black B, the following histochemical reagents were applied to fresh hand-cut sections: DMB reagent (0.5% solution of 3,4-dimethoxybenzaldehyde in 9% HCl), which forms a red reaction product with condensed tannin precursors (Mace and Howell 1974); and Millon's reagent as modified by Bakker (1956). With this stain, coloured nitroso derivatives of any phenols become evident (Sawidis 1998). For polysaccharide staining, sections of fixed or fresh material were treated with periodic acid – Schiff's reagent (PAS) according to Nevalainen et al. (1972) and examined by LM (Sawidis et al. 2000; Al-Tardeh et al. 2006, 2007).

Morphometry

For the morphometric evaluation of the relative volume of the histological components of the bulb scales, a transparent sheet bearing a square lattice of point arrays, 10 mm apart, was laid over light micrographs of bulb scale cross sections (×100; two micrographs for each bulb scale from five bulbs). The point-counting technique analysis was then applied (Steer 1981; Al-Tardeh et al. 2006). All statistical tests were performed using the statistical software package SPSS for Windows (version 11.5.1, SPSS Inc., Chicago, Ill.). Differences in means of anatomical and morphological variables were assessed using the analysis of variance (ANOVA). Correlation analysis was used to examine relationships among plant tissue variables.

Results

Morphoanatomical features of the bulb

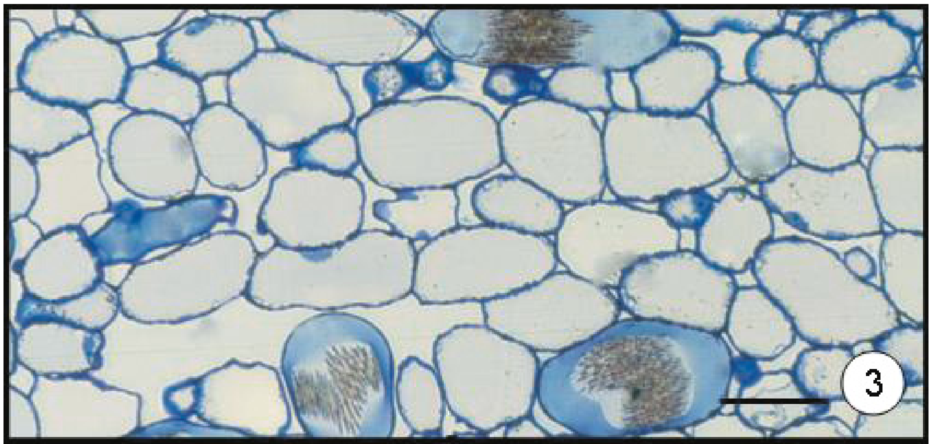
Bulb size correlates positively with bulb age and how many the bulb scales there are, i.e., the bigger bulb in size, the older in age and the more bulb scales in number. The bulb is covered by multiple-layered tunics (Fig. 1), a physical barrier for plant protection from environmental hazards. Thicknesses of bulb scales vary according to their ages and order within the bulb. However, the median axis of the bulb scale is the thickest and the margins are the thinnest (Fig. 1).

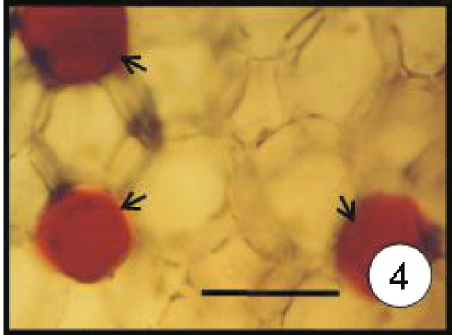
The bulb scales are covered with a smooth cuticle (12 ± 4 µm thick). The epidermal cell walls are evenly thickened. Cells are very similar, compactly arranged, and global to oval, and possess rounded margins (Fig. 2). The abaxial epidermis is slightly thicker (periclinal) than the adaxial epidermis. The bulb scales in cross section show a diversity of storage cells (Fig. 2). The ground tissue of the bulb scales is composed of larger cells that are thin walled and empty irregularly shaped, reflecting a water-storing character. Thick-walled assimilatory idioblast cells containing raphide bundles (profiles) within central vacuoles are present among ordinary ground tissue cells (Fig. 2). The cells containing raphides are circular, oval, polygonal, irregularly shaped, and two to six times longer than the neighboring ones as viewed in longitudinal section, whereas in cross section they are more or less the same diameter. Observations of hand-cut sections under polarized light reveal open bundles of calcium oxalate needles that are 432 ± 54 µm long (*n* = 250). Moreover, the ground tissue of bulb scales possesses circular to oval assimilatory mucilage cells (Fig. 2). The vascular bundles are collateral, scattered, and numerous. Sclerenchyma fibers are associated with both xylem and phloem in larger bundles. However, in smaller bundles, the sclerenchyma is associated with the phloem only, and the xylem is subtended by parenchyma

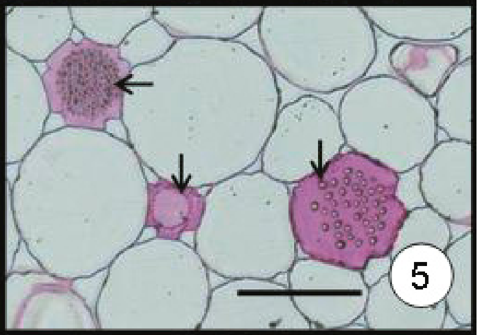
Morphologically, the bulb has a shortened stem called the basal plate that has one or more apical meristems and is enclosed by several fleshy bulb scales. During sectioning of the basal plate, it is obvious that basal plate tissues are the hardest (woody) and possess adventitious root initials (Fig. 1). The basal plate possesses storage cells containing raphide bundles within their central vacuoles. These cells are oriented in different directions. The parenchyamatous cells are of different shapes, i.e., circular, polygonal, elongated, and cubical (Fig. 3).

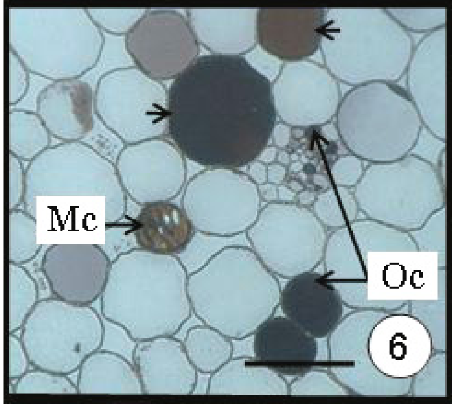
Histochemistry

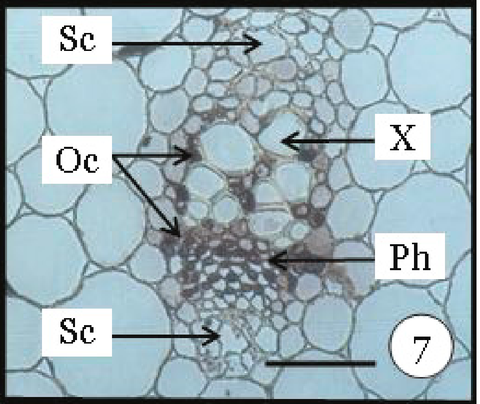
The red color intensity of cells in the mesophyll of bulb scales is variable in free-hand sections stained with Schiff's reagent (arrows, Fig. 4). These cells contain soluble polysaccharides in their large vacuole, which in some cases is more clearly seen after cells are plasmolysed. The idioblastic cells containing raphide bundles also react positively with Schiff's reagent (arrows, Fig. 5).

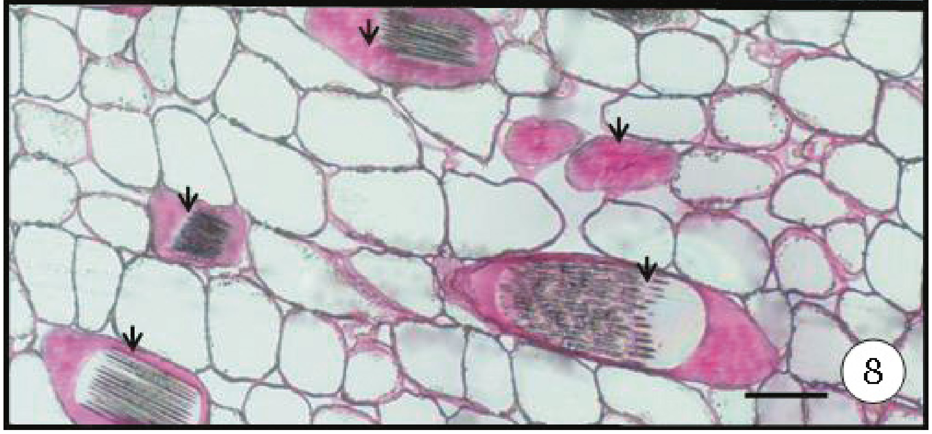












When semithin or hand-cut sections of bulb scales are treated with Sudan black B, numerous cells appear stained intensely brown to black (Fig. 6). Parenchyma cells containing lipophilic substances occur in the vascular cylinder (Fig. 7). Oil cells occur sporadically as solitary idioblasts and they do not differ greatly in size from their neighboring cells. These oil cells accumulate abundant oil insoluble in water. The oil idioblasts are rounded and almost devoid of cytoplasmic content (arrows, Fig. 6). Finally, oil droplets occurring in the cytoplasm react positively with this stain. Some of the basal plate cells also react positively with Schiff's reagent, which is evident in the presence of polysaccharide content. All cells containing raphide bundles react positively with this stain (Fig. 8).

Morphometry and reserves allocation

A morphometric analysis (Table 1) was carried out to explain the relationship between the bulb-scale reserve contents and their contributions to the total bulb-scale volume. The middle of the bulb (almost the third bulb scale) contains a considerable relative volume of the cells containing polysaccharides (12.91 ± 2.43%) and the highest level of lipid- (21.92 ± 2.43%) and mucilage- (9.34 + 1.03%) containing cells. The middle of the bulb is the most efficient part in storing reserves, because the total relative volume of its storage cells is 50.66%. The basal plate contains the highest relative volume of polysaccharide contents (15.00 ± 1.62%) and raphide inclusions (13.09 ± 1.67%). Finally, the lipids are almost absent from the outermost part of the bulb and the basal plate (around 0 %) (Table 1).

Water status

The water status within the bulb parts shows minor fluctuation through the stages of the plant's annual life cycle (Table 2). The highest water content (91%) was found in the central bulb scale (first bulb scale) during the active phase. The lowest water content (57%) was recorded for the same bulb-scale zone during the dormancy phase. The bulb scales show a high capacity for water storage in their tissues, especially those of the middle region of the bulb. This is obvious when the water content during the time of reproduction is compared with that of the dormant bulb scales. It is evident that the water content of the basal plate is the most stable throughout the year.

Discussion

Like other plant species (Brouillet and Simon 1979; Hume and Cavers 1983; Pantis 1993), *U. maritima* exhibits resource allocation patterns that are the result of both their genotype and their environment (Pfosser and Speta 2004). Moreover, plants with underground storage organs occur most commonly in dry coastal areas of the Mediterranean, where a strong winter rainfall pattern is combined with periodic drought and soils of low nutrient status. In these situations, a subterranean life form enables a plant to avoid drought and to carry substantial fractions of its nutrient resources from one growing season to the next (Rees 1981; Pate and Dixon 1982).

Like other perennial geophytes (Ruiters et al. 1993), the bulb's size and age is a determining factor for the ability for reproductive development. In such geophytes with hysteranthous leaves, accumulation of storage reserves is a prerequisite for flowering (Dafni et al. 1981; Ruiters et al. 1993). In the case of *U. maritima*, the plant reaches critical mass and is able to flower after 5–6 years of development from seed. (Pascual-Villalobos and Fernandez 1999). This species possesses large underground biomass and (or) reserve resources as required by the "reserve-pulse" model (Noy-Meir 1973). Changes of below- and above-ground biomass allocation synchronize the plant's phenological development with the seasonality of the Mediterranean climate (Sawidis et al. 2005). Analogous variations in these adaptations are reported for other perennial geophytes from Japan (Kawano et al. 1982) and South Africa (Ruiters et al. 1993).

The bulb content of reserves such as glycosides (cardiac glycosides) of the bufadienolide type (Kopp et al. 1996), anthocyanins (Vega et al. 1972), flavonoids (Fernandez et al. 1972), fatty acids, polysaccharides (Spies et al. 1992), and calcium oxalate (Cogne et al. 2001) varies considerably over the year. The highest values seem to occur in late spring, just after senescence of the leaves. This species keeps its nutrients in situ in the bulb components, minimizing energy cost associated with synthesis, breakdown, and translocation of storage compounds. This adaptation has also been reported for other geophytes (Chapin et al. 1990; Walton et al. 2007).

From the histochemical point of view, the mucilage of the cells containing raphide needles is polysaccharide, since it stains red with Schiff's reagent. The mucilage idioblasts associated with the vascular bundles and the epidermis, generally, have been regarded as water storage cells and are, thus, adaptively significant in warm habitats (Sawidis 1998). The mucilage has a substantial water-binding capacity due to its many hydroxyl groups and especially the carboxy groups of galacturonic acid (Goldstein and Nobel 1991). Hygroscopic polysaccharides such as mucilage can bind 51 times their weight of water when hydrated in vivo (Nobel et al. 1992). On the other hand, the cells that reacted positively with Sudan black B and the oil cells are located around the phloem cells, presumably to protect them from herbivores and insects.

Raphides, or needle-shaped crystals of calcium oxalate, usually occur in the cells of *U. maritima* adventitious roots (Al-Tardeh et al. 2006), leaves (Al-Tardeh et al. 2007), and bulb parts. The basal plate seems to be the active centre; therefore it needs extra protection, which could be demonstrated by the mechanical and chemical protection of the raphide inclusions (Table 1), the bulb scales, and the tunics. The relationship between calcium ion absorption and oxalic acid synthesis in plants is most probably established in order for the ionic balance in tissues to be maintained (Bosabalidis 1987). On the other hand, calcium content in dormant bulbs may be viewed as an osmoregulatory adaptation to drought during the dry, warm summer period (Levitt 1980). Raphides produce mild inflammation and irritant contact dermatitis when rubbed on the skin (Cogne et al. 2001; Salinas et al. 2001) and serve as a major defense against herbivores (Ruiz et al. 2002). Morphologically, their acicular shape is a critical component in proposed mechanisms for these defenses. In addition, twinning is an important factor in allowing plant cells to produce the raphide morphology (Arnott and Webb 2000). The polysaccharides content is strongly correlated with the raphides content (R = 0.78, n = 20), which might give a synergistic defense. The other stored defense compounds are thought to act against microbial agents (March et al. 1991), herbivores (Ruiz et al. 2002), rodents (Fitzpatrick 1952; Verbiscar et al. 1986*a*), fungi (Miyakado et al. 1975), and insects (Pascual-Villalobos and Fernandez 1999; Pascual-Villalobos 2002).

Scilliroside, the major toxic glycoside, occurs in all plant parts including the flowers, stalk, leaves, scales, and especially the roots and core of the bulbous part (Verbiscar et al. 1986*b*). This corresponds with our results that the middle

Table 1. Relative volumes (%) of the histological components with storage characteristics in the bulb scales of the bulb and the basal plate of *Urginea maritima* (mean ± SD, $n = 10$).

	Relative volumes of the storage cells (%)			
Storage cells	First bulb scale	Third bulb scale	Seventh bulb scale	Basal plate
Cells containing polysaccharides	5.56±1.72	12.91±2.43	6.59±1.76	15±1.62
Cells containing lipids	14.75±2.54	21.92±2.43	6.34±2.96	Zero
Idioblastic cells containing raphides	5.85±3.01	6.49±1.47	5.38±1.98	13.09±1.67
Cells containing mucilaginous material	No*	9.34±1.03	No*	No*
Total	25.664	50.66	18.31	28.09

*Not calculated because the relative volumes were very low and in some cases could be zero.

Table 2. Water contents of the bulb scales and the basal plate during the life cycle at the stage of leaf emergence (29 November 2006), at the mature leaf stage (2 January 2006), and at dormancy (dormant bulb) (12 July 2006) (mean ± SD, $n = 5$).

	Water content (%)		
Bulb part	At leaf emergence	At leaf maturation	At bulb dormancy
First bulb scale*	73.33	90.98	60.91
Second bulb scale	89.48	75.86	57.23
Third bulb scale	78.48	74.63	75.79
Fourth bulb scale	71.79	74.24	69.74
Fifth bulb scale	70.27	75.47	69.84
Sixth bulb scale	70.19	79.21	68.36
Seventh bulb scale	69.92	81.52	69.75
Eighth bulb scale	71.66	83.98	65.29
Tunics	00.00	00.00	00.00
Basal plate	70.54	77.23	75.63
The bulb†	73.96±6.4	79.24±5.5	67.5±5.5

*The bulb scales are in the order from one to eight followed by the tunics and the basal plate (see Fig. 1).

†Mean ± SD of the water content of the whole bulb.

of the bulb contains the highest content of resources, especially, the mucilaginous material and (or) glycosides (cardiac glycosides) of the bufadienolide type (Kopp et al. 1996). The bulb is not completely protected from herbivores and high temperatures at the soil surfaces because it is half buried in the soil. Correspondingly, the presence of a large number of glycosides (scilliroside) is considered an adaptive strategy to protect the plant from herbivores and environmental hazards.

One of the prominent features of the Mediterranean climate is its periodicity, to which *U. maritima* responds by synchronizing the annual development of its biological cycle (Al-Tardeh et al. 2006, 2007). As stated by Evans et al. (1992), survival during drought is ultimately dependent on the maintenance of cell turgor. This species is vulnerable to dehydration as witnessed by a visible shrinkage of older bulb scales, which are eventually altered to tunics. However, the tunics seem to be an adaptive strategy to avoid water loss by reducing both transpiration and overheating. Moreover, the species proves to be very efficient in storing water during the long summer drought. When the values of the water content in the upper part of the soil profile vary around 0%, the bulb remains hydrated and turgid with a water content >67.5%. The growing flower bud might be a sink for this water, which is supplied from the basal plate and bulb scales (Kamenetsky et al. 2003) because leaf spouting depends on the external water supply (Dafni et al. 1981; Al-Tardeh et al. 2007).

The tunic of *U. maritima* is a scale that has been totally modified as the bulb matures. The tunic provides protection against disease infection and mechanical damage to the outer scales and the basal plate that initiates the adventitious roots. It is well known that when the tunic is extremely hard and unbroken, such as in the tulip, it can restrict root growth. Moreover, it could have a chemical effect as well. The removal of the tunic enhances respiration and (or) aeration of the unplanted bulb of *Iris hollandica* Hort. (Kamerbeek 1962).

In conclusion, our results suggest that the different constituent bulb parts of *U. maritima* may serve different ecological functions in terms of their resource content, thus, differing in their importance for these functions. The bulb of *U. maritima* is well adapted and synchronized to the Mediterranean climate. The adaptive strategies are (*i*) the development of a semisubterranean life form as a primary avoidance of drought and for preservation of nutrients from herbivores and environmental hazards; (*ii*) the presence of cells containing lipids, polysaccharides, and oils; (*iii*) the presence of cells containing raphide needles; (*iv*) the presence of cells with water-storing character; (*v*) the presence of idioblast mucilage cells and (or) glycosides; (*vi*) the tightly packed epidermis; (*vii*) the smooth cuticle; and (*viii*) the presence of the tunics.

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